Genetic Diversity Patterns in Japanese Soybean Cultivars Based on Coefficient of Parentage

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ABSTRACT

Japan is a historical center of genetic diversity for soybean [*Glycine max* (L.) Merr.], but diversity of modern Japanese cultivars is not well characterized. The objectives of this study were to quantify genetic diversity of Japanese cultivars via coefficient of parentage (CP), determine the relative importance of breeding factors in explaining that diversity, and incorporate results into a practical guide for management of diversity. All 86 public Japanese cultivars released and registered during 1950 to 1988 were subjected to CP and multivariate analysis. The mean CP for the 86 cultivars was low (0.04), indicating a potentially high degree of diversity in Japanese breeding. Eighty percent of all pairs of cultivars were completely unrelated by pedigree. The low mean CP for the cultivars was attributed to a continual incorporation of unique Japanese land races into the genetic base over time, to the introduction of foreign germplasm from China and the United States and Canada (US-CAN) as breeding stock, and to limited exchange of germplasm among Japanese breeding programs. Cluster analysis was an effective discriminator of diversity. Six clusters were identified which had a mean CP value equivalent to that of half-sibs or greater. These clusters encompassed a total of 54 cultivars, explained 57% of the variation in the CP relations, and had few ancestors in common. Each cluster was derived primarily from only a few programs. Backcrossing and full-sib matings were absent in Japanese pedigrees and, thus, clusters were formed primarily from parent-offspring, full-sib, and half-sib relations. Cultivar attributes such as growing region, release era, maturity designation, and developing institution did not elucidate strong patterns of pedigree diversity. In practical breeding, one may maximize the chances of finding good specific Japanese × Japanese or Japanese × US-CAN crosses by choosing Japanese cultivars from a wide array of Japanese clusters rather than sampling extensively within a cluster.

CROP DIVERSITY IS ESSENTIAL to sustainable food production. The use of diversity in the form of resistance to diseases and insects, for example, has been a cornerstone of successful crop production in the past century (Campbell et al., 1999, p. 532). The primary developer of crop diversity for modern breeding was the ancient farmer. For millennia, farmers practiced on-farm breeding by noticing and saving beneficial genetic variants as they arose during production. Initial genetic variants derived from on-farm breeding facilitated the adaptation and spread of crops to a wide array of climates, soil types, and domestic uses, increased drastically the hectarage upon which subsequent on-farm breeding was practiced and resulted, ultimately, in a global reservoir of diversity. The thousands of genetic variants preserved in this way form the basis for modern cultivar improvement.

An important example of on-farm breeding success in soybean is cyst nematode (*Heterodera glycines* Ichinohe) resistance. Almost all cyst nematode resistance genes in modern U.S. cultivars trace their lineage directly from a few farmer-developed cultivars in China. These resistant cultivars were added to germplasm preservation banks after 1940, incorporated into modern breeding programs in the 1950s, and resulted in the release of the first resistant elite cultivars in the 1960s (Caviness, 1992). More than 30 000 accessions from on-farm soybean breeding are preserved in the germplasm collections of the USA, China, and Japan (Miyazaki et al., 1995a; Palmer et al., 1996; Xu et al., 1999).

While the importance of crop diversity is being recognized increasingly in agriculture, it is also true that diversity itself is being reduced in the farmer's field for many crops. A common scenario in agriculture is one where old cultivars and land races are replaced by new cultivars which are more closely related to each other than to the genetic materials they replaced (Ehrlich and Wilson, 1993). Soybean cultivars in the USA and Canada (US-CAN) provide a clear example of this trend, where cultivars today are more closely related than those grown 40 yr ago, and have an average pedigree relationship equivalent to that of half sib in the midwestern and southern growing regions (Gizlice et al., 1993). While this inbreeding in soybean has posed no obvious barrier to current sustainable soybean production in the USA (Specht et al., 1999), it is clear that the genetic diversity in applied breeding is much less than that available in the global germplasm collections. Reduced diversity is a potential problem for long-term soybean improvement and a concern with regard to genetic vulnerability.

In contrast to the trend in the USA, 75 yr of Chinese soybean breeding has not produced a sizable increase in the relationships of cultivars, even through yield gain has been substantial (1–2% per year) (Cui et al., 1998). On average, current Chinese cultivars share less than 2% of their genes in common, on the basis of CP analysis (Cui et al., 2000b). The CP between pairs of cultivars is the probability that a random allele at a random locus in one cultivar is identical by descent to a random allele at the same locus in another cultivar (Malécot, 1948; Kempthone, 1957). The successful maintenance of diversity in modern Chinese soybean breeding has been attributed to a continual infusion of new germplasm into applied programs and a strong tendency to avoid the mating of close relatives (Cui et al., 2000a,b).

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In Japan, the relatedness of modern soybean cultivars and the changes in their CP relationships over recent decades is not quantified. However, researchers have noted the general distinctness of Japanese cultivars in comparison with those of the US-CAN and China. Zhou et al. (2000) reported that the Japanese genetic base was quite distinct from that of China or the US-CAN on the basis of pedigree analyses, and that cultivars from three major growing regions in Japan shared little ancestry in common with each other. The DNA marker analysis of modern cultivars from Japan has confirmed the distinctness of Japanese cultivars from those of China and the US-CAN (Thompson et al., 1997; Nelson et al., 1998; Carter et al., 2000).

Carter et al. (2000) proposed that modern cultivars from Japan, China, and the USA may serve as important contrasting and mutually beneficial reservoirs of genetic diversity for future applied breeding. Multi-year field tests in the USA indicated that modern Japanese cultivars may carry important agronomic genes for breeding (Carter et al., 2000). Elucidation of patterns of diversity among Japanese cultivars should aid the preservation and efficient use of Japanese cultivar diversity both within the Japanese soybean breeding pool and in its cross breeding with Chinese, US-CAN, and other elite materials. The objectives of this study were to quantify genetic diversity in Japanese cultivars, determine the relative importance of regions, release eras, maturity groups, and developing institutions (i.e., breeding programs) in explaining that diversity, and incorporate results into guidelines which promote efficient use of genetic diversity found in Japanese cultivars.

MATERIALS AND METHODS

The origin, pedigree, year of release, Japanese maturity rating, and intended end use were compiled for all 86 public Japanese soybean cultivars released and registered during 1950 to 1988 (Fukui and Arai, 1951) (S. Miyazaki, personal communication, 1999). These cultivars were developed in 11 distinct breeding programs and represented up to five cycles of breeding in Japan since World War II. Cultivars were rated for maturity at Clayton, NC, in 1994 and 1995 in comparison to standard U.S. cultivars. Each cultivar was assigned to a primary growing region of Japan on the basis of the location of the developing institution, where regions were defined as northern Japan (NJ, Hokkaido Island), central Japan (CJ, Honshu Island), and southern Japan (SJ, Kyushu Island) (Table 1) (Zhou et al., 2000). Four release eras were defined as 1950s (1950–1959), 1960s (1960–1969), 1970s (1970–1979), and 1980s (1980 to 1988). The CP matrix for the 86 cultivars was computed by a FORTRAN program as described by Zhou et al. (2000). Briefly, pedigree information was compiled into a data base and checked exhaustively for errors. A first subroutine of the program assigned codes to ancestors and progeny. An overwrite file added CP relations that were not easily represented in the data base. The second subroutine used the output from the first subroutine and the overwrite file to calculate the CP matrix. The CP between individuals X and Y was calculated as $CP_{XY} = pCP_{XA} + qCP_{XB}$, where Y was the progeny of A and B, X was a second strain but not a descendent of Y, and p and q were the percentage contribution of A and B to Y. If two parents A and B contributed equally to Y, then the above formula was simplified to $CP_{XY} = 1/2$ $(CP_{XA} + CP_{XB})$ which was the usual case.

Multidimensional Scaling and Cluster Analysis of Coefficient of Parentage

Multidimensional Scaling Analysis

Multidimensional scaling (MDS) analysis provides approximate relations of items such as cultivars in a few dimensions on the basis of their relations in a larger matrix of similarities, such as a CP matrix (SAS, 1992). In this study, the MDS procedure was applied directly to the original CP matrix for the 86 Japanese cultivars, employing the same options as Gizlice et al. (1996) (SIMILAR = 1, COFF = IDENTITY, and LEVEL = ABSOLUTE). By trial and observation, we found that an analysis with 40 dimensions produced an output with an excellent fit to the 86×86 CP matrix, as measured by stress or badness-of-fit criterion (2.0%) and by R^2 (0.98). Stress is a measure of the extent to which a geometrical representation falls short of a perfect match with the original CP matrix (Kruskal, 1964). Zero percent stress represents a perfect fit and 20% indicates a poor fit. The R^2 was calculated from the comparison of the original CP matrix with predicted values derived from the MDS coordinates. For easy graphical representation of relationships among cultivars, a two-dimensional MDS analysis was employed to produce coordinates for two-dimensional plots (Fig. 1, Fig. 2).

Cluster Analysis

The FASTCLUS procedure, a non-hierarchical cluster analysis, was applied to the MDS-derived Euclidean coordinate data on the basis of 40 dimensions (SAS, 1985b). To find an optimum number of clusters, the utility of four to 15 clusters was evaluated in 12 independent analyses (Gizlice et al., 1996). The mean CP within and among clusters was computed for each analysis by the MEANS procedure of SAS (SAS, 1985a).

The relation of various factors in explaining diversity patterns was computed through regression analyses of clusters, growing regions, release eras, maturity estimates, and breeding programs on the original CP matrix as described by Gizlice et al. (1996) and Cui et al. (2000b). Models with single and combinations of variables were fitted by the GLM procedure. The R^2 was used to assess the importance of each variable (SAS, 1985b). For regression analysis of the cluster factor, cultivars that were not part of an acceptable cluster were combined into one cluster for easy computation.

RESULTS AND DISCUSSION

Genetic Diversity among Regions in Japan

The mean CP value for the 86 cultivars was low (0.04), indicating a potentially high degree of diversity in Japanese breeding. This value was slightly higher than that reported for Chinese soybean cultivars (0.02), but much lower than that for US-CAN cultivars (0.13–0.17) (Gizlice et al., 1993; Sneller, 1994; Cui et al., 2000b). The low mean CP for Japanese cultivars reflected the fact that 80% of all pairs of cultivars were completely unrelated within the boundaries of available pedigree data. Inspection of pedigrees showed that backcrossing and full-sib matings were completely absent in Japanese pedigrees, which contributed, in part, to the low relationship among cultivars.

Although Japanese cultivars exhibited a low overall

Table 1. Cultivar code, name, developing institution, Japanese accession code, region (northern Japan, NJ, central Japan, CJ, and southern Japan, SJ), year of release, maturity group (MG), pedigree-based cluster, and intended end use for 86 public Japanese soybean cultivars released during 1950 to 1988.

Code	Name	Location or station†	Japanese accession code	Region	Year of release	Flower color‡	Pubescence color‡	Approx. U.S. MG§	Japanese MG¶	Pedigree-based cluster#	Intended end use††
C01	Aki Sengoku	Kumamoto (Aso)	000 33076	SJ	1962	W	G	IX	Vc		tofu
C02	Akishirome	Kyushu (Kumamoto)	000 33205	SJ	1979	P	G	V	IIIc	6	tofu
C03	Akiyoshi	Kumamoto (Aso)	000 33095	SJ	1963	P	G	VIII	IVc	6	tofu
C04	Aso Aogari	Kumamoto (Aso)	000 33099	SJ	1963	P	T	VII	Vc		fodder, green manure
C05	Aso Masari	Kumamoto (Aso)	000 33069	SJ	1954	W	T	IX	Vc	6	tofu
C06	Aso Musume	Kumamoto (Aso)	000 33172	SJ	1956	P	G	VIII	Vc		tofu
C07	Bon Minori	Ibaraki (Ishioka)	000 31753	CJ	1961	W	T	I	IIa	4	tofu, miso
C08	Daruma Masari	Akita (Odate)	000 30949	NJ	1951	W	T	I	IIc		miso, tofu
C09	Dewa Musume	Tohoku (Kariwano)	000 31360	CJ	1977	P	G	II	IIc	2	tofu
C10	Enrei	Nagano (Kikyogahara)	000 32237	CJ	1971	P	G	III	IIc	4	tofu, misco, nimame
C11	Fuji Musume	Saga	000 33018	SJ	1961	P	G	I	IIa	5	tofu
C12	Fuji Otome	Ibaraki (Ishioka)	000 32542	CJ	1966	P	G	IV	IIb	4	tofu, miso
C13	Fujimijiro	Nagano (Kikyogahara)	000 32235	CJ	1964	P	G	III	IIc	4	tofu, miso
C14	Fuku Shirome	Tohoku (Kariwano)	000 31361	CJ	1985	W	G	II	IIb	3	tofu
C15	Fukumejiro	Ibaraki (Ishioka)	000 32540	CJ	1958	W	G	I	IIb		tofu, miso
C16	Fukunagaha	Hokkaido (Central)	000 30628	NJ	1981	W	G	II	IIa		nimame, tofu
C17	Fukuyutaka	Kyushu (Kumamoto)	000 33204	SJ	1980	P	G	VII	IVc		tofu
C18	Gogaku	Kumamoto (Aso)	000 33154	SJ	1967	P	G	VIII	IVc		tofu
C19	Hatsukari	Tohoku (Kariwano)	000 30952	SJ	1959	P	T	II	IIb		miso, tofu
C20	Higo Musume	Saga	000 32983	SJ	1965	P	T	00	IIa		tofu
C21	Himeshirazu	Nat. Inst. Animal Industry	000 74536	CJ	1970	P	T	VII	Vc	5	fodder, green manure
C22	Himeyutaka	Hokkaido (Tokachi)	000 30636	NJ	1976	P	Gl	I	Ib	1	nimame, tofu
C23	Hokkai Hadaka	Hokkaido (Tokachi)	000 30486	NJ	1958	W	G	00	Ia	1	tofu, miso
C24	Hougyoku	Kumamoto (Aso)	000 33073	SJ	1953	P	G	IX	Vc		tofu
C25	Hourai	Hokkaido (Tokachi)	000 30499	NJ	1965	P	T	0	Ib		tofu, miso
C26	Hourei	Nagano (Chushin)	000 74159	CJ	1987	P	G	II	IIb		tofu
C27	Hyuuga	Kumamoto (Aso)	000 33173	NJ	1969	P	G	I	IVc		tofu
C28	Karikachi	Hokkaido (Tokachi)	000 30478	NJ	1959	P	T	I	Ia	1	tofu, miso
C29	Karumai	Tohoku (Kariwano)	000 31329	CJ	1973	P	·	III	IIb	2	tofu
C30	Kitahomare	Hokkaido (Tokachi)	000 30554	NJ	1980	W	G	II	Ib	1	tofu, miso
C31	Kitakomachi	Hokkaido (Tokachi)	000 30637	NJ	1978	P	G	00	Ia		nimame, tofu
C32	Kitamusume	Hokkaido (Tokachi)	000 30530	NJ	1968	P	G	I	Ib	1	tofu, miso
C33	Kogane Daizu	Saga	000 33016	SJ	1958	P	T	0	IIa	5	tofu
C34	Kogane Jiro	Hokkaido (Tokachi)	000 30513	NJ	1961	P	G	0	Ib	1	tofu, miso
C35	Kokeshi Jiro	Ibaraki (Ishioka)	000 31766	CJ	1964	P	G	0	IIb	3	tofu, miso
C36	Komamusume	Hokkaido (Central)	000 30627	NJ	1982	P	G	I	Ib	1	nimame, tofu
C37	Kosuzu	Tohoku (Kariwano)	000 74956	CJ	1987	·	·	III	IIc		natto
C38	Misuzu Daizu	Nagano (Kikyogahara)	000 32231	CJ	1968	W	G	V	IIIc	2	tofu, miso, nimame
C39	Miyagi Oojiro	Nagano (Kikyogahara)	000 32673	CJ	1978	P	G	VI	IIIc		nimame
C40	Mutsu Mejiro	Tohoku (Kariwano)	000 30979	CJ	1965	P	G	I	IIb	1	tofu
C41	Mutsu Shiratama	Tohoku (Kariwano)	000 30981	CJ	1967	W	G	II	IIc		tofu, nimame
C42	Nagaha Jiro	Hokkaido	000 30485	NJ	1961	P	G	II	Ib	1	tofu
C43	Nakasenmari	Nagano (Kikyogahara)	000 32649	CJ	1978	P	G	V	IIIc	2	tofu, miso
C44	Nanbu Shirome	Tohoku (Kariwano)	000 31357	CJ	1977	P	G	II	IIc	2	tofu
C45	Nasu Shirome	Nagano (Kikyogahara)	000 32232	CJ	1968	W	G	III	IIIc	2	tofu, miso
C46	Nema Shirazu	Tohoku (Kariwano)	000 30818	CJ	1961	P	G	III	IIIb	2	tofu, nimame
C47	Oku Mejiro	Ibaraki (Ishioka)	000 31754	CJ	1961	P	T	IV	IIa	4	tofu, miso
C48	Oku Shirome	Tohoku (Kariwano)	000 31212	CJ	1972	P	G	II	IIc	2	tofu
C49	Ootsuru	Nagano (Chushin)	000 76831	CJ	1988	P	G	IV	IIIc	4	tofu, miso, nimame
C50	Orihime	Saga	000 33153	SJ	1967	P	G	0	IIa	5	tofu
C51	Oshima Shirome	Hokkaido	000 30492	NJ	1964	W	G	III	IIb	1	tofu, miso
C52	Raiden	Tohoku (Kariwano)	000 30819	CJ	1966	P	G	II	IIc	2	tofu
C53	Raikou	Tohoku (Kariwano)	000 31149	CJ	1969	P	G	II	IIc	2	tofu
C54	Sayohime	Saga	000 33017	SJ	1960	P	G	0	IIa	5	tofu

Continued next page.

Table 1. Continued.

Code	Name	Location or station†	Japanese accession code	Region	Year of release	Flower color‡	Pubescence color‡	Approx. U.S. MG§	Japanese MG¶	Pedigree-based cluster#	Intended end use††
C55	Shin Mejiro	Ibaraki (Ishioka)	000 31750	CJ	1954	P	G	II	IIb		tofu, miso
C56	Shinsei	Hokkaido (Tokachi)	000 30479	NJ	1961	P	T	0	Ia	1	tofu, miso
C57	Shiro Sennari	Nagano (Kikyogahara)	000 32543	CJ	1971	W	G	II	IIb		tofu, miso
C58	Shiromeyutaka	Nagano (Kikyogahara)	000 32236	CJ	1962	P	G	V	IIIc	4	tofu, miso
C59	Shirotae	Nagano (Kikyogahara)	000 32234	NJ	1965	W	G	VI	IIIc		tofu, niname
C60	Suzuhime	Hokkaido (Tokachi)	000 30638	NJ	1980	P	G	I	Ia	1	natto
C61	Suzukari	Tohoku (Kariwano)	000 74953	CJ	1985	P	G	II	IIc	2	tofu, niname
C62	Suzumaru	Hokkaido (Central)	000 74265	NJ	1988	P	G	0	Ib		natto
C63	Suzuyutaka	Tohoku (Kariwano)	000 74952	CJ	1982	P	G	III	IIc	2	tofu, miso
C64	Tachi Suzunari	Ibaraki (Ishioka)	000 31752	CJ	1960	W	T	II	IIb	4	tofu, miso
C65	Tachikogane	Tohoku (Kariwano)	000 74955	CJ	1983	P	G	II	IIb	2	tofu
C66	Tachinagaha	Nagano (Chushin)	000 74158	CJ	1986	P	G	IV	IIIc		tofu, miso, niname
C67	Tachiyutaka	Tohoku (Kariwano)	000 74954	CJ	1987	W	G	IV	IIc		tofu
C68	Tamahikari	Nagano (Kikyogahara)	000 32233	CJ	1971	P	G	V	IIIc		tofu, miso, niname
C69	Tamahomare	Nagano (Kikyogahara)	000 32650	CJ	1980	P	G	VI	IIIc	4	tofu, miso
C70	Tamamusume	Ibaraki (Ishioka)	000 31749	CJ	1950	W	Gl	II	IIa	3	tofu, miso
C71	Tanrei	Nagano (Kikyogahara)	000 32674	CJ	1978	P	G	III	IIb	4	tofu, miso
C72	Tokachi Kuro	Hokkaido (Tokachi)	000 30639	NJ	1984	P	T	I	Ib	1	niname, confection
C73	Tokachi Shiro	Hokkaido (Tokachi)	000 30480	NJ	1961	P	G	I	Ib	1	tofu, miso
C74	Toyokomachi	Hokkaido (Tokachi)	000 58916	NJ	1988	P	G	0	Ia		niname, tofu
C75	Toyomusume	Hokkaido (Tokachi)	000 30641	NJ	1985	P	G	I	Ib		niname, tofu
C76	Toyoshirome	Kyushu (Kumamoto)	000 33217	SJ	1985	P	G	VII	IVc	4	tofu
C77	Toyosuzu	Hokkaido (Tokachi)	000 30640	NJ	1966	P	G	I	Ib		niname, tofu
C78	Tsurukogane	Hokkaido (Central)	000 74264	NJ	1984	W	G	I	Ib		niname, tofu
C79	Tsurusengoku	Nat. Inst. Animal Industry	000 74535	CJ	1965	P	T	VIII	Vc		fodder, green manure
C80	Ugo Daizu	Akita (Odate)	000 30950	CJ	1952	P	T	II	IIc	4	miso, tofu
C81	Wase Kogane	Hokkaido (Tokachi)	000 30498	NJ	1964	P	G	0	Ib	1	tofu, miso
C82	Wase Shiroge	Tohoku (Kariwano)	000 30951	CJ	1956	P	G	0	IIb	4	miso, tofu
C83	Wase Shirome	Tohoku (Kariwano)	000 30982	CJ	1967	P	G	0	IIb	1	tofu
C84	Waseuzunari	Tohoku (Kariwano)	000 74957	CJ	1983	P	G	I	IIb	2	tofu
C85	Yuuhime	Hokkaido (Central)	000 30629	NJ	1979	P	G	I	Ib		niname, tofu
C86	Yuuzuru	Hokkaido (Central)	000 30630	NJ	1971	W	G	I	Ib		niname, tofu

† Location of developer and branch station given in parenthesis. Nagano (Kikyogahara) and Nagano (Chushin) were the names for the same station, but were used at different times. Only Nagano (Chushin) was used in the CP analysis.

‡ W = White; P = Purple; G = Gray; Gl = Glabrous; T = Tawny.

§ Maturity group was recorded from field tests at Clayton, NC, in 1994 and 1995.

¶ Japanese maturity group is designated in two parts: the first part, denoted by Roman numerals represents days from planting to flowering; the second part, denoted by English letters represents days from flowering to maturity (Fukui and Arai, 1951).

Six clusters were identified which encompassed 54 of the 86 Japanese cultivars. Other cultivars did not fall within a cluster.

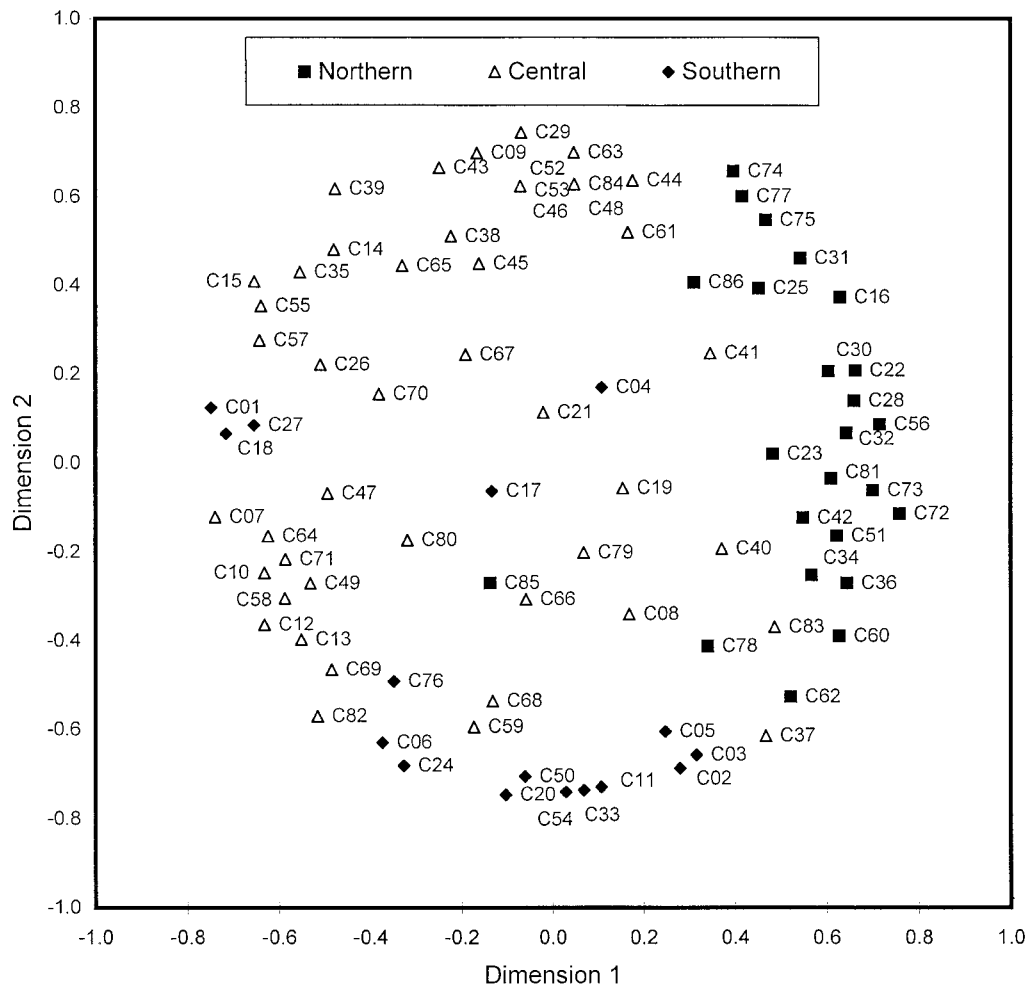†† Most Japanese cultivars were developed for food purposes. Niname is boiled mature soybean.

Fig. 1. Plot of coefficient of parentage (CP) relationship for 86 Japanese soybean cultivars released from 1950 to 1988. Coordinates for a cultivar were obtained from multidimensional scaling analysis employing two dimensions based on CP relations. The complement of the linear distances (1 − Distance) between any two cultivars estimates the coefficient of parentage between them. Distances ≥1 indicate no pedigree relationship between cultivars. For cultivar codes, see Table 1.

CP of 0.04, the mean CP within each of the three regions was slightly higher (0.13, 0.07, and 0.07 for the NJ, CJ, and SJ regions, respectively) (Table 2). The mean CP between regions was near zero (<0.02). Cui et al. (2000b) found a similar trend for China, where the mean CP of Chinese cultivars within each of the three major growing regions varied from 0.02 to 0.06 but was essentially zero between regions. A similar trend was also observed for US-CAN soybean cultivars, where the mean CP within southern and midwestern growing re-

gions was 0.23 and 0.18, respectively, while the mean CP between the two regions was only 0.04 (Gizlice et al., 1993).

The distinctness of regions with respect to pedigree may be related in part to maturity effects. In Japan, China, and the USA, regions differed markedly in the mean maturity of cultivars. Such maturity differences may have served as a natural reproductive barrier to pre-serve regional distinctions in pedigree despite breeder advances in hybridization technology and the availabil-

Table 2. Mean coefficient of parentage (CP) of soybean cultivars within and between the three growing regions of Japan: northern Japan (NJ), central Japan (CJ), southern Japan (SJ), number of released cultivars in each region, and mean U.S. maturity group.

	Growing region				Mean U.S. maturity group†	
Growing region	NJ	CJ	SJ	Released cultivars	Mean	Range
				no.		
NJ	0.133			24	1.2	−1 to 3
CJ	0.012	0.065		46	3.4	0 to 8
SJ	0.000	0.006	0.074	16	5.7	−1 to 9

† Maturity group was recorded from field tests at Clayton, NC, in 1994 and 1995. For ease of calculation and representation, maturity group data are presented in Arabic rather than standard Roman numerals, where 000 = −2, 00 = −1, 0 = 0, I = 1, II = 2, III = 3, etc. Decimal values do not refer to a maturity classification system known as relative maturity groupings employed by U.S. breeders. Rather, they reflect a simple average of traditional maturity group ratings. For example, the mean maturity of five cultivars of maturity group I and five cultivars of maturity group II is 1.5.
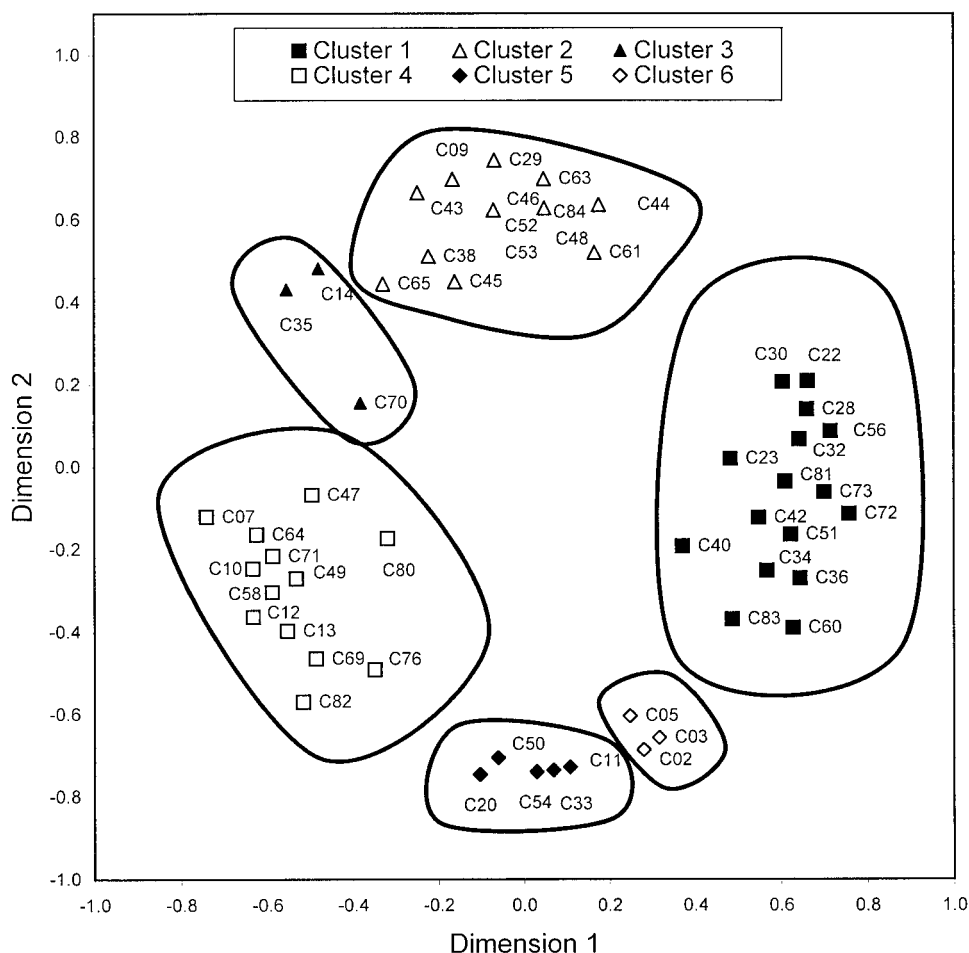
Fig. 2. Plot of coefficient of parentage (CP) relationship among six clusters representing 54 Japanese soybean cultivars released from 1950 to 1988. Coordinates for a cultivar were obtained from multidimensional scaling analysis employing two dimensions based on CP relations. The complement of the linear distances (1 − Distance) between any two cultivars estimates the coefficient of parentage between them. Distances ≥1 indicate no relationship. For cultivar codes, see Table 1.

ity of seed for mating. For example, mean U.S. maturity group classification for cultivars of the NJ, CJ, and SJ regions of Japan was I-II, III-IV, and V-VI, respectively (Table 2). The maturity distinction between cultivars of regions NJ and SJ may have been sufficient to limit breeders' opportunities to mate cultivars from these regions and develop elite breeding lines from them.

The low CP relations between growing regions in Japan could be visualized graphically by means of coordinates from a two-dimensional MDS analysis (Fig. 1). The NJ cultivars were separated from others by dimension 1, and SJ cultivars were separated roughly from CJ cultivars by dimension 2. The cultivars from CJ occupied more space in the graph than the NJ and SJ cultivars together, even though the number of cultivars from NJ and SJ together is similar to that from CJ. This indicated that CJ cultivars were perhaps more diverse in terms of pedigree than those from the other two regions. This notion was supported, in part, by the fact that the CJ region had a lower mean CP than did the NJ region (Table 2).

Table 3. Mean coefficient of parentage (CP) of Japanese soybean cultivars within and between the four release eras: 1950s (1950–1959), 1960s (1960–1969), 1970s (1970–1979), and 1980s (1980–1988), number of released cultivars in each region, and mean U.S. maturity group.

	Release era				Released	Mean U.S. maturity group†	
Release era	1950s	1960s	1970s	1980s	cultivars	Mean	Range
					no.		
1950s	0.021				13	3.2	−1 to 9
1960s	0.027	0.047			35	3.3	−1 to 9
1970s	0.014	0.041	0.034		16	3.4	−1 to 7
1980s	0.016	0.039	0.043	0.037	22	2.9	0 to 7

† Maturity group was recorded from field tests at Clayton, NC, in 1994 and 1995. For ease of calculation and representation, maturity group data are presented in Arabic rather than standard Roman numerals, where 000 = −2, 00 = −1, 0 = 0, I = 1, II = 2, III = 3, etc. Decimal values do not refer to a maturity classification system known as relative maturity groupings employed by U.S. breeders. Rather, they reflect a simple average of traditional maturity group ratings. For example, the mean maturity of five cultivars of maturity group I and five cultivars of maturity group II is 1.5.

Table 4. Japanese soybean cluster, number of cultivars for each cluster, mean CP within cluster based on the coefficient of parentage analysis, mean maturity group, and mean release year. Ranges appear in parenthesis for maturity group and release year.

Cluster	1	2	3
Primary region of origin†	NJ	CJ	CJ
Cultivars, no.	16	14	3
Mean CP within cluster	0.24	0.37	0.42
Mean maturity group‡	1.2 (−1 to 3)	3.1 (1 to 5)	2.0 (2 to 2)
Mean release year	1968 (1961 to 1984)	1974 (1961 to 1985)	1966 (1950 to 1985)
Breeding programs which contributed to a cluster§	Hokkaido (NJ, 2) Hokkaido (Central) (NJ, 1) Hokkaido (Tokachi) (NJ, 11) Tohoku (Kariwano) (CJ, 2)	Nagano (Chushin (CJ, 3) Tohoku (Kariwano) (CJ, 11)	Ibaraki (Ishioka) (CJ, 2) Tohoku (Kariwano) (CJ, 1)
	4	5	6
Primary region of origin†	CJ	SJ	SJ
Cultivars, no.	13	5	3
Mean CP within cluster	0.24	0.35	0.42
Mean maturity group‡	3.9 (1 to 7)	0.7 (−1 to 1)	7.9 (5 to 9)
Mean release year	1968 (1952 to 1988)	1962 (1958 to 1967)	1965 (1954 to 1979)
Breeding programs which contributed to a cluster§	Akita (Odate) (CJ, 1) Ibaraki (Ishioka) (CJ, 4) Nagano (Chushin) (CJ, 6) Tohoku (Kariwano) (CJ, 1) Kyushu (Kumamoto) (SJ, 1)	Saga (SJ, 5)	Kumamoto (Aso) (SJ, 2) Kyushu (Kumamoto) (SJ, 1)

† NJ = Northern Japan; CJ = Central Japan; SJ = Southern Japan.
‡ Maturity group was recorded from field tests at Clayton, NC, in 1994 and 1995. For ease of calculation and representation, maturity group data are presented in Arabic rather than standard Roman numerals, where 000 = −2, 00 = −1, 0 = 0, I = 1, II = 2, III = 3, etc. Decimal values do not refer to a maturity classification system known as relative maturity groupings employed by U.S. breeders. Rather, they reflect a simple average of traditional maturity group ratings. For example, the mean maturity of five cultivars of maturity group I and five cultivars of maturity group II is 1.5.
§ The number in parenthesis is the number of cultivars developed from that station.

Genetic Diversity among Contrasting Release Eras

Mean CP for Japanese cultivars would be expected to increase over cycles of breeding because breeders tend to use a limited number of elite lines from one cycle to generate the next. This practice tends to force the mating of relatives and drive CP upward (St. Martin, 1982). However, the mean CP for each release era was low and ranged only from 0.02 to 0.05. The CP between release eras was also low (0.01–0.04) (Table 3). The low mean CP of Japanese cultivars for all release eras reflected a continual expansion of the genetic base over approximately five cycles of breeding, through incorporation of new genetic materials. This trend for CP was similar to that found in China, but contrasted with the trend found for US-CAN release eras, where the mean CP for release eras increased steadily from 0.10 in the early 1950s to 0.17 in the early 1980s (Gizlice et al., 1993). The rising CP of US-CAN cultivars in succeeding eras reflected the almost closed nature of the US-CAN genetic base which was eroded over time through the mating of relatives (Gizlice et al., 1993). The contrasting trends in CP between U.S. and Japanese breeding can be described in population genetics terms, where US-CAN breeding had a relatively smaller effective population size and, thus, a faster rise in CP over time (St. Martin, 1982).

Cluster Analysis of Breeding Patterns

The MDS analysis with 40 dimensions produced an excellent Euclidean representation of the CP matrix (R^2 = 0.98 and stress = 0.02) (Kruskal, 1964). The coordinates produced from this MDS analysis were subjected to 12 separate nonhierarchical FASTCLUS anal-

yses with the number of clusters ranging from 4 to 15 (SAS, 1992). The best cluster analysis was identified as that which assigned the most cultivars to acceptable clusters. An acceptable cluster was defined as having (i) at least three cultivar members, (ii) a mean CP comparable to that of half sibs or greater, and (iii) a mean CP with other clusters that was less than 0.05. Similar definitions have been employed in the analysis of CP in other soybean data sets (Gizlice et al., 1996; Cui et al., 2000b). In this study, the FASTCLUS analysis using 14 clusters assigned the most (54 cultivars) cultivars into six acceptable clusters and was the only cluster analysis retained here (Tables 1 and 4).

The mean within-cluster CP for the six clusters was at least 0.24. Among the six acceptable clusters, three clusters were composed primarily of cultivars from the central region, one primarily from the northern region and two clusters from the southern region (Table 4). The clear genetic distinction of the clusters could be visualized graphically by means of coordinates from the two-dimensional MDS analysis (Fig. 2). Pedigree analysis revealed that clusters contrasted sharply, that they originated from different breeding programs, and that each was derived from a rather narrow genetic base. The five most important ancestors of each cluster contributed from 67 to 100% of their cluster's genetic base (Table 5). Among the five most important ancestors in a cluster, the first two usually contributed at least 50% of the genes of that cluster. Examination of the 12 most important ancestors from the six clusters (i.e., the two most important contributors for each cluster) revealed that they were also important to the overall genetic base of Japanese soybean, contributing at least 3% to a region (Zhou et al., 2000). This result indicated clearly that cluster analysis identified cultivar groups that were meaningful and had breeding importance.

Table 5. Five most important ancestors and their relative genetic contribution (GC) to six nonhierarchical clusters of Japanese soybean cultivars.

Cluster	Ancestor name	GC†	Ancestor name	GC	Ancestor name	GC	Ancestor name	GC	Ancestor name	GC	Cumulative GC
		%		%		%		%		%	%
1	Ooyachi	24.3	Daizu Hon 326	22.6	Kamishunbets Zairai	14.2	Shi Li Huang	8.0	Shirosota	7.1	76.2
2	Geden Shirazu	43.7	Nangun Takedate	19.1	Mandarin (Ottawa)	6.1	Houjaku	5.5	Yama Shiratama	5.5	79.9
3	Shirosaya	34.6	Nezumi Saya	29.6	Kimusume	25.9	Geden Shirazu	4.9	Satour Mame	4.9	99.5
4	Ani	25.9	Shiroge	21.0	Kuro Daizu	10.5	Yougetsu	4.7	Shiro Hachikoku	3.5	65.6
5	Matsuura	33.3	Takiya	27.8	Choutan	13.9	Karihantakiya	13.9	Shirosaya	11.1	100
6	Kuma	29.2	Ooita Aki Daizu 2	29.2	Shiro Daizu 3	25.0	Hato Goroshi 12	16.7			100

† Genetic contribution of an ancestor to a cluster was defined as the fraction of genes in the cluster that could be traced to the ancestor. Coefficient of parentage was used to estimate the contribution and was calculated as the average CP between an ancestor and all members of the cluster.

The fact that almost all cultivars within a cluster originated from one growing region was consistent with the observation that regions were very distinct in terms of pedigree and CP. In keeping with geographical origins, clusters also contrasted for maturity, with most of the early maturing clusters derived from the NJ region (Table 4). A very early maturing cluster from the SJ region, Cluster five, was the only clear exception to this trend.

Cultivars with exotic ancestors in their pedigrees fell into distinct clusters. Eight of the twelve NJ cultivars with Chinese pedigree fell into cluster one. Four of six cultivars with elite U.S. materials in the pedigree fell into two clusters (three and four). No clear pattern was found with regard to the relationship between the intended end-use of cultivars and cluster assignments.

Genetic Diversity among Contrasting Maturity Groups

Exact U.S. maturity groupings are not well established for most Japanese cultivars. Maturity group estimates employed in this study, for example, were derived from only 2 yr of field observation in North Carolina. Thus, it is possible that some of the maturity group designations employed here were in error by as much as one full maturity group. To minimize the effect of this problem on analysis of maturity, genotypes from neighboring maturity groups were combined into larger maturity groupings prior to statistical analysis of maturity effects (Table 6). The mean CP for each combined maturity group ranged from 0.05 to 0.13 and CP between combined maturity groups ranged from 0.00 to 0.06 (Ta-

ble 6). Thus, CP was lower and genetic diversity was greater within maturity groups than has been reported for U.S. cultivars, reflecting the general trend for Japanese breeders to avoid the mating of close relatives. (Gizlice et al., 1996).

Although regions of Japan differed greatly in the average maturity of their cultivars, each region also exhibited a range in cultivar maturity. For example, while most members of cluster four were maturity group III through V and from the CJ region, the cluster also contained an early- and a late-maturing entry (maturity group 0 and VII) (Table 4). The occurrence of a wide range of maturity for cultivars and clusters within a region may be related to the need to produce soybean in multiple crop rotation systems. Employment of cultivars with a wide range of maturity groups and grown in multiple cropping systems would ensure a continual supply of fresh seed and guard against the disastrous impact of sporadic bad weather on seed quality and yield. This rationale may explain the occurrence of a very early maturing cluster among the otherwise later maturing cultivars of the SJ region, where the growing season is longest. In the SJ region, two soybean ecotypes are grown: summer and fall soybean (S. Miyazaki, personal communication, 1999). The summer ecotype is planted in spring and harvested in summer, while the fall ecotype is planted in early summer and harvested in late fall.

Genetic Diversity among Breeding Institutions

Eleven breeding institutions developed the 86 cultivars used in this study. Among them, three breed-

Table 6. Mean coefficient of parentage (CP) of Japanese soybean cultivars among and within approximate U.S. maturity groups.

Maturity group†	Maturity group					Released cultivars
	−1 to 1	2 to 3	4 to 5	6 to 7	8 to 9	
						no.
−1 to 1	0.062					32
2 to 3	0.031	0.079				29
4 to 5	0.011	0.057	0.081			11
6 to 7	0.001	0.011	0.030	0.048		7
8 to 9	0.000	0.004	0.010	0.038	0.125	7

† Maturity group was recorded from field tests at Clayton, NC, in 1994 and 1995. For ease of calculation and representation, maturity group data are presented in Arabic rather than standard Roman numerals, where 000 = −2, 00 = −1, 0 = 0, I = 1, II = 2, III = 3, etc. Decimal values do not refer to a maturity classification system known as relative maturity groupings employed by U.S. breeders. Rather, they reflect a simple average of traditional maturity group ratings. For example, the mean maturity of five cultivars of maturity group I and five cultivars of maturity group II is 1.5. To minimize the effect of bias from a single maturity group on analysis of maturity, genotypes from neighboring maturity groups were combined into larger maturity groupings prior to statistical analysis of maturity effects.

Table 7. Mean coefficient of parentage (CP) of soybean cultivars within and between the 11 breeding programs of Japan, number of released cultivars in each breeding program, and mean U.S. maturity group.

| Breeding Program | NJ | | | CJ | | | | | SJ | | | Released cultivar | Mean U.S. maturity group | |
	1	2	3	4	5	6	7	8	9	10	11		Mean	Range
												no.		
1. Hokkaido (Tokachi)	0.191											16	0.9	00 to 2
2. Hokkaido (Central)	0.053	0.049										6	1.4	0 to 2
3. Hokkaido	0.180	0.135	0.500									2	2.5	2 to 3
4. Akita (Odate)	0.000	0.000	0.000	0.000								2	1.5	1 to 2
5. Ibaraki (Ishioka)	0.000	0.000	0.000	0.023	0.112							8	2.7	1 to 4
6. Nagano (Chushin)	0.010	0.002	0.010	0.022	0.090	0.116						15	4.5	2 to 6
7. National Institute Animal Industry	0.000	0.000	0.000	0.000	0.000	0.000	0.000					2	7.5	7 to 8
8. Touhok (Kariwano)	0.025	0.017	0.016	0.016	0.011	0.045	0.000	0.144				19	2.4	0 to 4
9. Kyuushu (Kumamoto)	0.000	0.000	0.000	0.004	0.013	0.040	0.000	0.001	0.042			3	6.7	5 to 7
10. Kumamoto (Aso)	0.000	0.000	0.000	0.000	0.000	0.007	0.016	0.002	0.042	0.152		8	8.4	7 to 9
11. Saga	0.000	0.000	0.000	0.000	0.009	0.000	0.000	0.002	0.000	0.000	0.350	5	0.7	00 to 1

ing institutions were located in the NJ, five in the CJ, and three in the SJ regions. These breeding programs spanned a wide latitude (roughly from 31–45.5° N) equivalent in range to that of Toronto, Canada and Jacksonville, FL in North America. As a result, cultivars released from these programs contrasted greatly in mean maturity (from U.S. maturity group I–IX) (Table 7). Because of the wide range in maturity for the breeding programs, germplasm developed by one program was often unadapted for another and, thus, germplasm exchange among them was minimal. The low germplasm exchange was reflected statistically in a CP less than 0.1 between most programs. Only programs from the NJ region had CP relations slightly greater than 0.1 (0.15–0.18). The wide range in maturity among Japanese breeding programs also limited cooperative breeding trials among programs. Although formal regional cooperative yield tests among US-CAN breeders have been integral to breeding progress, no such practices developed in Japan except for the NJ region (S. Miyazaki, personal communication, 2001).

One might expect that limited exchange among breeding programs could force an increase in CP relations within programs. However, the CP of cultivars within breeding programs was generally low. Minimal exposure to genetic products from other Japanese programs may have caused breeders to turn their breeding attention more toward land races and exotic germplasm for breeding stock. Both within- and between- breeding program CP relations were lower in Japan than in US-CAN (Gizlice et al., 1996).

Relative Importance of the Diversity Patterns

To establish the relative importance of various factors in determining genetic diversity patterns in Japanese cultivars, we employed a series of regression analyses and compared R^2 values. Growing regions, although clearly distinct in pedigree, explained only 14% of the total variation in cultivar relationships. The four release eras, though quite distinct in terms of CP, accounted for only 1% of the variation in CP. Maturity group and breeding program effects explained more variation than did growing regions or release eras, but accounted for only 21 and 28% in the CP matrix, respectively. In contrast, the six clusters we identified accounted for

57% of the variation. Thus, cluster analysis identified the major diversity pattern in Japanese cultivars with respect to pedigree. Cluster analysis was also found to be the best discriminator of diversity patterns in CP for Chinese and US-CAN cultivars (Gizlice et al., 1996; Cui et al., 2000b). Regression of combinations of breeding factors against CP did not have an appreciable effect on R^2 values in comparison to single factor analyses. Regression of cluster plus breeding program, cluster plus region, cluster plus release era, and cluster plus maturity group against CP accounted for 72, 62, 65, and 68% of the variation, respectively. Other combinations accounted for less than 40% of the variation.

Use of Foreign Germplasm in Japanese Breeding

While Japanese breeders have relied extensively on Japanese landraces to infuse new genes into breeding, they also employed exotic materials from China, the US-CAN, and elsewhere (Zhou et al., 2000). Fourteen cultivars were derived from seven Chinese ancestors or old cultivars and six from US-CAN stocks (Table 8). Among those, seven Chinese ancestors or old cultivars, 'Ouhoushu', 'Shika 4', and 'Mansoukin' were widely grown cultivars in the Northeast of China before 1960 (Ouhoushu is also referred to as 'Huang Bao Zhu' in Chinese; Shika 4 is designated 'Zi Hua 4 Hao' in Chinese; and Mansoukin is designated 'Man Cang Jin' in Chinese) (Miyazaki et al., 1995b; Cui et al, 1999). Two other Chinese ancestors of Japanese cultivars, 'Kingen' ('Jin Yuan' in Chinese and a parent of Mansoukin) and 'Si Li Huang' (a parent of Ouhoushu) were also important ancestors in Chinese breeding, and together accounted for 11.6% of Chinese soybean genetic base (Cui et al., 2000a).

The US-CAN germplasm 'Harosoy' (Weiss and Stevenson, 1955), 'Lee' (Johnson, 1958), and 'Pickett', also known as NC1-2-2 (Brim and Ross, 1966), released from 1955 to 1966, were used to develop six Japanese cultivars. Harosoy and Lee represent 17.7% of the genetic base of U.S. soybean (Gizlice et al., 1994). NC1-2-2 is believed to be a single plant selection from NC-1, a high protein germplasm population derived from two U.S. breeding lines. Among these six cultivars developed from U.S. materials, two ('Dewa Musume' and 'Tamahomare') were direct offspring of either Harosoy or

Table 8. Utilization of exotic germplasm in Japanese soybean cultivar development. First progeny cultivars were derived from foreign breeding stock and designated by codes which appeared in Table 1.

Country of origin	Foreign cultivar or breeding line used in original cross†	Chinese name for the foreign cultivar or breeding line from China‡	First progeny cultivar derived from foreign stock (code, release year and growing region in parenthesis)§	First release of Japanese cultivar derived from a foreign stock	Estimated year in which foreign stock was used in a cross to produce a Japanese cultivar¶
China	Koushurei 235	Gong Zhu Ling 235	Daruma Masari (C08, 1951, CJ), Hatsukari (C19, 1959, CJ)	1951	1933
	Ouhoushu	Huang Bao Zhu	Nagaha Jiro (C42, 1961, NJ), Tokachi Shiro (C73, 1961, NJ), Oshima Shirome (C51, 1964, NJ), Tsurukogane (C78, 1984, NJ)	1961	1951
	Shika 4	Zi Hua 4 Hao	Kogane Jiro (C34, 1961, NJ), Wase Kogane (C81, 1964, NJ)	1961	1951
	Yore		Bon Minori (C07, 1961, CJ)	1961	1943
	Mansoukin	Man Cang Jin	Tokachi Shiro (C73, 1961, NJ)	1961	1951
	Kokuiku 44	Guo Yu 44	Kitahomare (C30, 1980, NJ), Fukunagaha (C16, 1981, NJ)	1980	1954
	Wase Hadaka		Suzumaru (C62, 1988, NJ)	1988	1970
U.S. and Canada	Harosoy		Dewa Musume (C09, 1977, CJ), Suzuyutaka (C63, 1982, CJ), Tachiyutaka (C67, 1987, CJ)	1977	1967
	Lee		Tamahomare (C69, 1980, CJ)	1980	1970
	Pickett (NC1-2-2)		Hourei (C26, 1987, CJ)	1987	1970
Korea	Shirosota		Mutsu Mejiro (C40, 1965, CJ), Wase Shirome (C83, 1967, CJ)	1965	1955
	PI 84751		Suzuhime (C60, 1980, NJ)	1980	1970
Sakhalin Island	Karafuto 1		Toyokomachi (C74, 1988, NJ)	1988	1978

† Three U.S. genotypes were used as parents to develop five first progeny cultivars, and they can be traced to six ancestors. PI 84751 was originally from Korea and introduced to Japan via USA. It was used as a parent because of its resistance to cyst nematode.
‡ Ouhoushu was selected from Si Li Huang. Shika 4 was selected from Hakubi and Mansoukin was a progeny of Kingen and Ouhoushu.
§ First progeny cultivars were defined as those for which there were no available cultivars between them and corresponding ancestors. Fourteen Japanese cultivars were released from a breeding program using Chinese ancestors, of which 12 were first progeny cultivars. Six Japanese cultivars were released from a breeding program using U.S. or Canadian genotypes, of which five were first progeny cultivars. Code, year of release, and growing region of first progeny cultivars appear in parentheses.
¶ The year was estimated via the following rule: 10 yr from cross to release of cultivar and 8 yr from cross to development of breeding line.

Lee. Five of the six cultivars were developed in the CJ and the remaining one in the SJ region.

Japanese cultivars developed from US-CAN materials were all released after 1977, whereas most cultivars derived as first progeny from Chinese parents were released before 1960, indicating a change over time in the source of exotic germplasm for breeder use. If one assumes that a cross was made 10 yr before release of a cultivar and 8 yr before release (or use) of a breeding line from that cross, then almost all Chinese ancestors were used as parents before 1955 and all other exotic ancestors, except one, were used after 1965 (Table 8). This switch coincided with historical events. From 1931 to 1945, Japan occupied northeast China, providing Japanese breeders with access to Chinese germplasm. Commercial trade and presumably germplasm exchange continued between Japan and China until the Korean conflict in the early 1950s, but was minimal thereafter for some years (Schaller, 1985).

In contrast, the Japanese did not develop an apparent interest in U.S. germplasm until around 1958, when Japanese agronomists and horticulturists visited USDA germplasm collection maintenance facilities (J. Creech, personal communication, 2000). However, the trigger for Japanese breeders' use of US-CAN germplasm was the liberalization of soybean import in 1961 (S. Miyazaki, personal communication, 1999). As a result of this policy change, domestic soybean production lost competitiveness and decreased dramatically. Therefore, Japanese breeders were dispatched to the USA and Europe to study advanced soybean breeding programs. On the basis of their studies, Japanese programs were reorganized and strengthened. These developments, plus the availability and extensive characterization of U.S. germplasm for traits such as soybean cyst resistance, the more difficult access to Chinese germplasm after the Korean conflict of the 1950s, and the incomplete characterization of germplasm in the Chinese collection at that time induced Japanese soybean breeders to turn their attention to US-CAN germplasm.

It is interesting to note that germplasm flow from Japan to the USA began in the 1920s, when two USDA plant exploration groups were sent to Japan. Two soybean specialists, W.J. Morse and P.H. Dorsett joined one expedition (Creech, 2000). They traveled through Japan, Korea, and northeast China and brought back approximately 3000 soybean accessions. Among them, several became ancestors of US-CAN breeding, such as PI 80837 from Japan, 'Kanro' from South Korea, and PI 88788 from China.

Implications to Plant Breeding

Japanese soybean breeding has focused mainly on seed quality traits such as yellow hilum, large seed, high protein content, and cooking quality in addition to high yield. Some of these characters may be critically important not only to Japanese breeding, but to breeding efforts in the USA, China, and elsewhere. The results of the CP analysis reported here provide guidelines which should promote the efficient use of that genetic diversity which is present in Japanese cultivars. This information

will be useful not only to Japan, but to China, the USA, and other countries which develop soybean cultivars.

The available data suggest that Japanese soybean breeding has remained robust in terms of genetic diversity. The close genetic relationships between modern cultivars have been minimized through avoidance of mating of close relatives and through continual additions of germplasm to the genetic base. Full sib and backcross matings were absent in Japanese pedigrees. Also, in contrast to soybean breeding in the USA, Japanese breeding had no land mark cultivars such as Lee, 'Williams', and Harosoy to dominate pedigrees of subsequent cultivars and drive CP upwards. The clearest patterns of diversity in Japanese cultivars were identified by cluster analysis. Breeding programs and maturity groupings were associated with CP to a lesser degree.

Breeding patterns identified here may assist the Japanese breeders in the efficient selection of parental stock for making selections. Avoidance of matings within clusters would be a practical approach to continued maintenance of diversity in Japanese breeding. Manjarrez-Sandoval et al. (1997) found that a CP between parents greater than that of half sibs (0.25, the average relation of Japanese clusters identified here) often means small genetic variance for yield in their progeny and, thus, slow breeding progress. Also, increased exchange among breeding programs would be a desirable breeding approach in the maintenance of diversity. Elite breeding lines from contrasting Japanese breeding programs often have CP relations much lower than 0.25, affording breeders the opportunity to capitalize upon gains made in each program, without sacrificing diversity.

For soybean breeding in the US-CAN, the original genetic base was narrow, and new cultivars were developed through intensive selection upon what has remained a narrow base. Introduction of exotic germplasm to broaden diversity has been slow in U.S. breeding because of a focus on short-term breeding gains rather than maintenance of diversity. Also, it is not clear to most breeders how best to select germplasm to broaden their programs. A benefit of the present study is in the assistance of US-CAN breeders in the selection of Asian cultivars with which to broaden the US-CAN genetic base. Clusters identified in this study may represent successful breeding endeavors in Japan, and thus, they may offer good choices for parental stock. We suggest that breeders may maximize their chances of finding good specific US-CAN by Japanese crosses by (i) choosing a wide range of U.S. parental stock, (ii) choosing Japanese parental stock from multiple clusters, multiple breeding programs, or otherwise from diverse pedigrees, (iii) avoidance of Japanese cultivars with U.S. pedigree, and (iv) by selecting Japanese cultivars with a desirable phenotype such as high yield.

Extensive evaluation of Japanese cultivars in the USA via the SAVE (Soybean Asian Variety Evaluation) project revealed that several Japanese cultivars were relatively higher yielding, with no clear pattern to high yielding ability in terms of regional origin, release era, or cluster assignment (Carter et al., 2000). Cultivars from the SJ region were slightly higher yielding, relative to

controls, than those from other regions. Surprisingly, older cultivars were often as high yielding as more recently released Japanese cultivars. Japanese soybean breeding objectives and/or interaction between genotype and environment may have caused this result.

The CP analysis provided here is not the only guide available to breeders for preservation or increase of genetic diversity in applied programs. Analysis of DNA marker populations may shed light on the most efficient use of desirable Japanese cultivars in future breeding. However, the low pedigree relation among Japanese cultivars, the low pedigree relation of Japanese cultivars to U.S. and Chinese cultivars, the large number of ancestors in the genetic base of Japanese breeding, and the lengthy pedigree history of soybean breeding in Japan (since World War II) all suggest that the reservoir of genetic diversity represented by Japanese cultivars is a promising area for future breeding research.

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